Simulating Molluscan Shell Pigment Lines and States: Implications for Pattern Diversity

BY

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(1 Plate)

INTRODUCTION

It would be easier to understand the tremendous variety of molluscan shell pigment patterns if a common cellular basis for it were known. Several analyses (Wrigley, 1948; Waddington & Cowe, 1969; and Seilacher, 1972) suggest that the same mechanism controls the patterns in various species. How different patterns might develop from common cellular states within a species can be seen in the evidence (Lindsay, MS) that the divaricate pigment patterns of *Lioconcha castrensis* (Linnaeus, 1758) (Bivalvia: Veneridae) develop from different sequences of eight standard pigmentation states in the mantle.

Divaricate pigment patterns are lineages of units in which pairs of lines or edges diverge over the surface of the valve. Lindsay (MS) presented evidence that *Lioconcha castrensis* assembles four major kinds of pattern, each from a characteristic unit made of radial and divergent lines (Figure *1*). These lines, in turn, were interpreted (Lindsay, MS) to represent different on-off combinations of three properties: 1) ability of pigmentation zones (Emberton, 1963) to deposit pigment; 2) to move tangentially in the margin of the mantle; and 3) the actual direction of movement. Switching movement off, for example, converts a divergent line to radial, and turning pigment deposition off ends either line. This subunitary approach makes it evident that pattern variation may depend on standard binary pigment states and transitions controlled at several cellular levels in the mantle edge.

The present report demonstrates by computer simulation, that these states and pigment lines can also account for interspecific differences among *Lioconcha castrensis* and two species of gastropod, *Oliva porphyria* (Linnaeus, 1758) and *Conus marmoreus* Linnaeus, 1758. These simulations suggest that the regulatory states which deposit radial and divergent lines may be versatile agents of shell pigment pattern variation across a broad phylogenetic range of molluscs.

METHODS

Specimens of *Lioconcha castrensis* were kindly loaned by R. T. Abbott, Delaware Museum of Natural History; K. R. Boss, Museum of Comparative Zoology; G. M. Davis, Academy of Natural Sciences of Philadelphia (ANSP) and J. Rosewater, National Museum of Natural History (NMNH). Others are from the author's collection (DTL).

Shell pigment patterns were simulated with a program named Shelpat, written in Fortran 4 for the Control Data Corporation Cyber 74 computer at the University of Georgia. Shelpat simulates appositional growth of patterns by printing vertical and diagonal lines row by row down the computer page. Shelpat scans each row for lines. When it encounters one, it identifies the line as vertical or diagonal and decides with a random number generator whether the line continues growing, stops, or in the case of diagonals, branches.

Shelpat approaches pattern variation parsimoniously. It attempts to infer from patterns the minimum controls necessary to produce acceptable simulations of as many different patterns as possible. The program generates variation from four sets of standard control variables, rather than using new variables for each species. Each set represents a standard regulation that inspection of shell patterns and simulations has shown to be necessary for patterns to develop. The modeler simulates intra- and interspecific variation among these regulations by assigning different values to the variables.

Shelpat's control variables are based on observations (Lindsay, MS) from *Lioconcha castrensis* that new divergent lines branch from old ones, that radials begin on divergent lines, and that lines may grow, branch, or terminate (see Figure *1*). The first set of variables contains probabilities that govern the fate of diagonal lines. Shelpat compares these values to uniformly distributed random numbers and prints long terminal lines, short branching ones or others depending on the choice of values. The second set controls the length of vertical lines by specifying the mean and variance of a normal distribution curve. Large values give long variable verticals, small values short uniform lines.

The third variable concerns simultaneous termination of neighboring radial lines in triangles. When given the value "on," this variable causes a terminal vertical line to end neighboring lines and when "off," terminating diagonals end neighboring radials instead. The difference allows Shelpat to print right triangles and isosceles triangles. The last set of variables decides whether converging lines terminate or branch. It contains probabilities for these events which Shelpat compares with uniform random numbers.

RESULTS

Different combinations of all four variables produce patterns that resemble those of *Lioconcha castrensis, Oliva porphyria,* or *Conus marmoreus.* A portion of printout corresponding to two tents from an open pattern in *L. castrensis* appears in Figure 2a. Control values were selected for relatively short diagonal lines which terminate and branch with the same frequency. Short, relatively uniform vertical lines simulate the irregular inner edges of these tents, except where divergent lines terminate neighboring verticals. The third value was "off" and the fourth, though not effective in this example, favored termination of convergent lines.

Figure 2b simulates isosceles triangles from a closed pattern to *Lioconcha.* All control variables retained the same values, except that the length of vertical lines was increased to fill the triangles.

Simulations of halved patterns from *Lioconcha* appear in Figure 2c. Here, the control values produced a long diagonal line by suppressing branching and termination. The mean and variance gave intermediate lengths to vertical lines and the third variable was turned "on" to terminate them. As a result, the first vertical line to terminate under the normal curve stops its neighbors and forms a right triangle. The next vertical to end under the curve produces the second triangle, and so on. (The mean and variance also control the number of neighbors terminated.) Though irrelevant in this example, variable four still favored termination of converging lines.

Figure 2d represents a simulation of a brush from a wide pattern in *Lioconcha.* Branching and termination were suppressed again in the diagonal lines, and the mean and variance have been increased for verticals. Simultaneous termination of verticals has been turned "off" and convergence is the same as before. Consequently, Shelpat prints a long diagonal line from which radials extend for normally distributed distances.

Other combinations of control values cause Shelpat to simulate *Oliva porphyria* and *Conus marmoreus. Olivà porphyria* displays patterns of divergent lines which branch from each other and end when they intersect (Figure *3*b). Radial lines are reduced or absent. Shelpat produces such patterns (Figure *3*b) when the control variables favor long, branching diagonal lines which terminate at intersections, and when the mean and variance for vertical lines are zero. Simultaneous termination of verticals is irrelevant under these conditions. *Conus marmoreus* requires nearly opposite values (Figure *3*a). In this case, very long diagonal

Explanation of Figures *1* to *3*

Figure *1*: Pattern and subunits from *Lioconcha castrensis.* Patterns on the valves at the top of the figure consist of radial and divergent lines organized into the subunits at the bottom. (A) Open patterns (NMNH 247597) consist of tents; (B) closed (ANSP 254601), isosceles triangles; (C) halved patterns (ANSP 206389A), right triangles; and (D) wide patterns (ANSP 53475A), brushes. The units differ according to the number of divergent lines, the length of radial lines, and whether the radials end simultaneously. Evidence for this subunitary basis is given in Lindsay, MS. Arrows identify parts of patterns simulated by computer in Figure *2*.
Bar = 1 cm

Figure *2*: Simulations of *Lioconcha* shell pigment patterns.
Bar = 1 cm
The bar does not apply to simulations, which were printed at 8 lines per inch. (A) A pair of tents from a simulation of open patterns and comparable pattern from NMNH 247597. See Figure *1* for the whole valve of this and other specimens. (B) A string of isosceles triangles from a simulation of closed patterns and a sequence from ANSP 254601. (C) Right triangles simulating halved patterns and a similar sequence from ANSP 206389A. (D) A brush and similar sequence from wide patterns in ANSP 53475A.

Figure *3*: Simulations of patterns in *Conus* and *Oliva.* Bar = 1 cm. (A) *Conus marmoreus* (inset) and printout. DTL (unknown provenance). (B) *Oliva porphyria* (inset) and printout. DTL (unknown provenance)

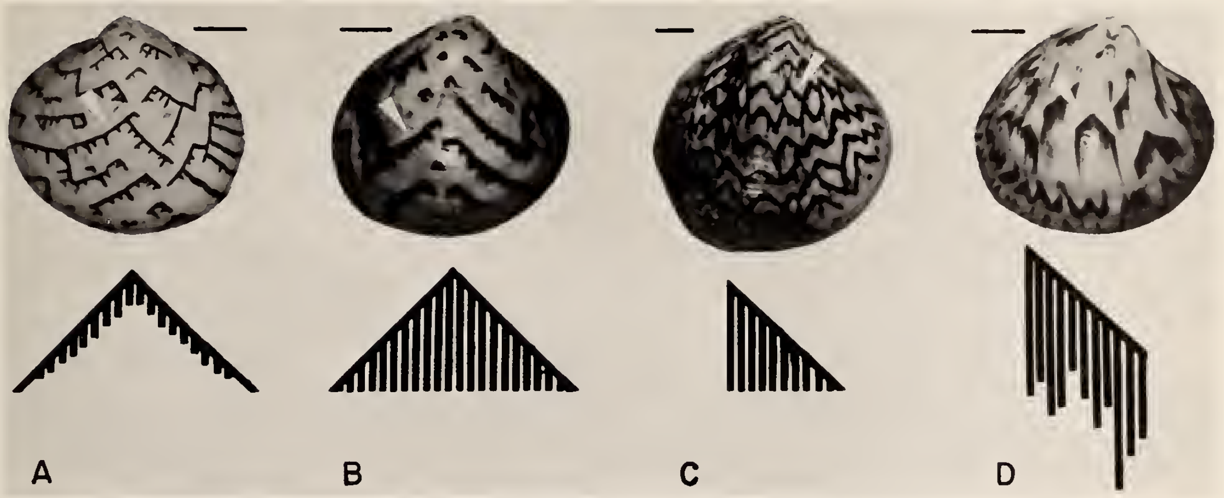

Figure *1*

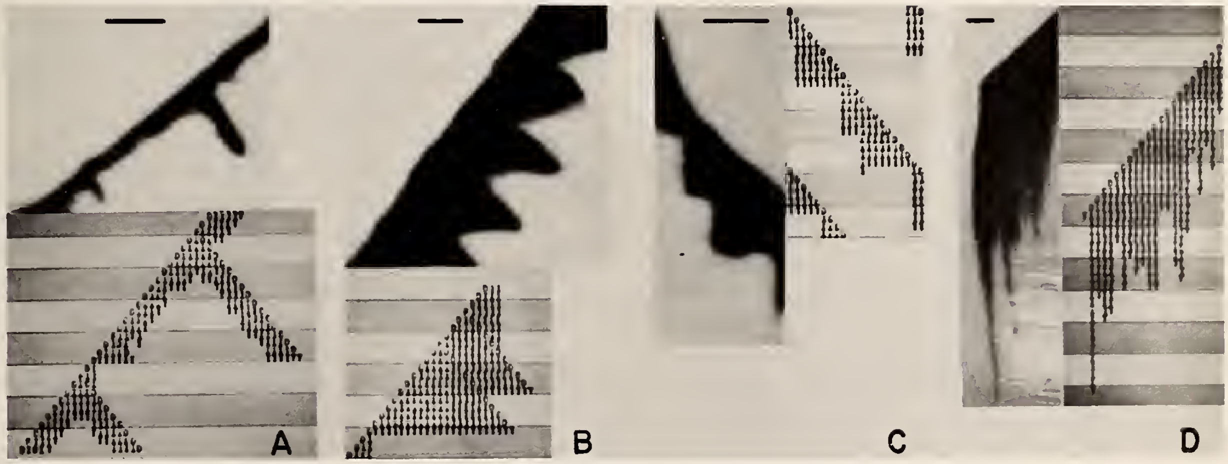

Figure *2*

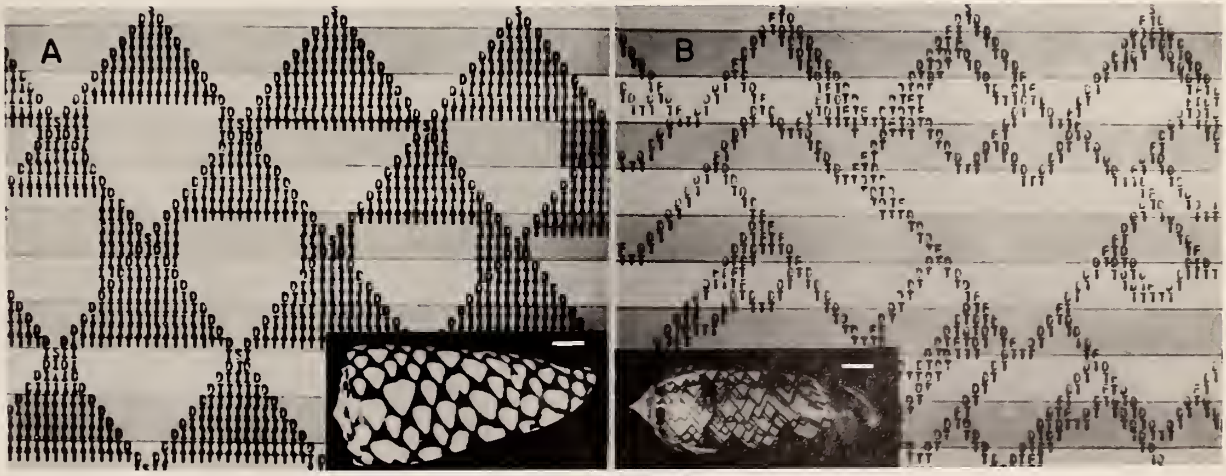

Figure *3*